

ECHINODORUS IN THE AMERICAN TROPICS

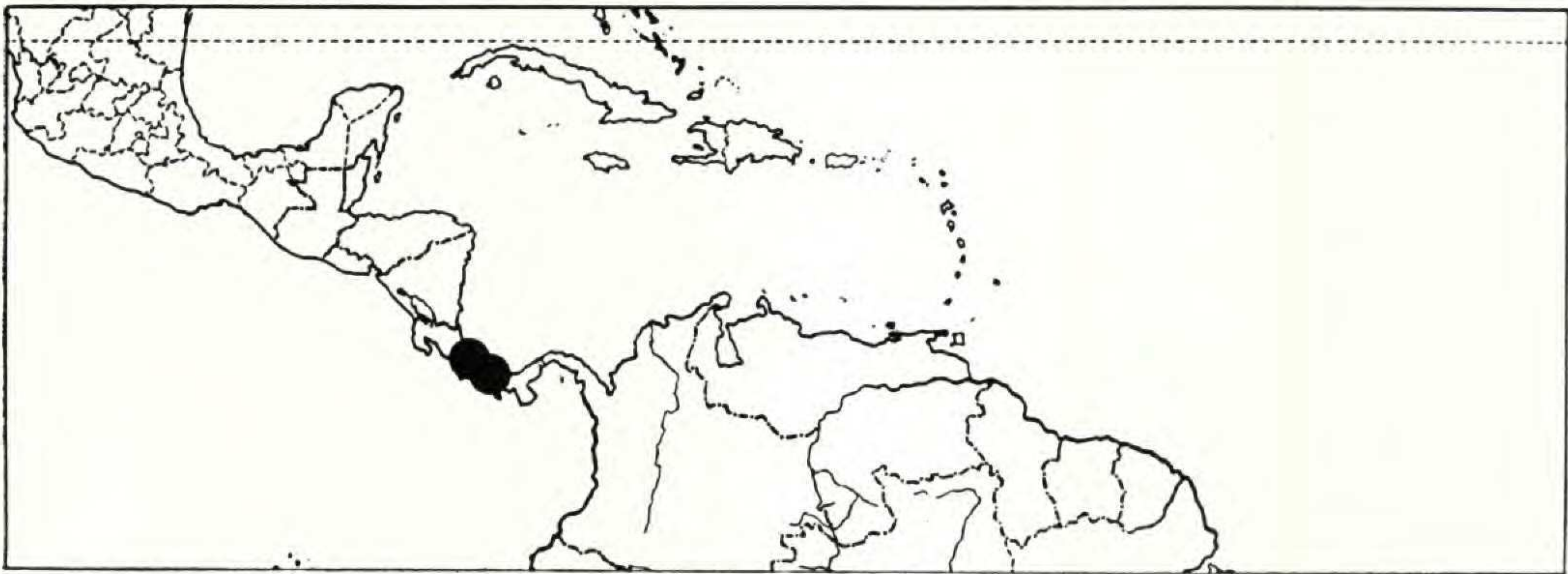
NORMAN C. FASSETT

(Continued from p. 188)

15d. *E. TENELLUS*, var. **latifolius** (Seubert) Fassett, n. comb. *Alisma tenellum* forma *latifolia* Seubert in Mart. Fl. Bras. **3**, pt. 1: 195, t. 13, fig. 2, nutlet and plant to left. 1848.

Southern Brazil to Venezuela, West Indies, and northern Central America (Map 13d) **Guatemala**: Lake Zotz, Petén, 18 May 1933, *Lundell 3293* (F); Dept. Jalapa, Potrero Carrillo, 13 miles northeast of Jalapa, alt. 1500–1700 m., 12 December 1939, *Steyermark 33098* (F); Dept. Alta Verapaz, bogs near Santa Cruz, along road to San Cristóbal, alt. about 1350 m., 16 April 1941, *Steyermark 42754* (F); Dept. Alta Verapaz, large swamp just east of Yactic, alt. 1300 m., 20 February 1942, *Steyermark 43977* (F). **Honduras**: in bog, in pine forest, El Achote, near Siguatepeque, Dept. of Comayagua, alt. 1500 m., 18 February 1928, *Standley 56099* (US, F). **Jamaica**: growing in swamp, Cornwall, St. Elizabeth, 18 July 1915, *Harriss 12095* (GH, F, MO, NY, US); Cornwall swamp, near Locovia, 1915, *Perkins* (NY). **Dominican Republic**: Prov. de la Vega, prope Tarabacoa in paludosis 550 m. alt., June 1912, *Fuertes 1666* (F, GH, NY, US); Llano Costero, Prov. Sto. Domingo, Cuenca, edge of laguna, 6 January 1929, *Ekman 11025* (US). **Porto Rico**: Laguna Yeguada near Vega Baja, 24 March 1922, *Britton, Britton & Brown 6773* (F, NY, US); muddy marsh, vicinity of San Juan, 11 & 12 February 1914, *Britton & Cowell 1483* (GH, NY, US); Martin Peña, 12 February 1914, *Johnston 1314* (NY). **Venezuela**: Tovar, 1854–55, *Fendler 1358* (GH); La Trinidad de Maracay, at an altitude of 440 meters, State of Aragua, January–February 1913, *Pittier 5844* (NY, US); in morass, El Limón, near Maracay, Aragua, 19 January 1922, *Pittier 10104* (GH, NY, US); Anzoátegui, headwater of Río Guanipa, 28 December 1940, *Pittier 14637* (US). **British Guiana**: herb, on edge of drying pond, basin of Rupununi River, lat. about 2° 52', 25 & 26 October 1937, *Smith 2285* (F, MO, NY, US). **Bolivia**: Reyes, alt. 1000 ft., October 1921, *Rusby 1540A* (NY, US). **Brazil**: Lagoa Santo, Minas Geraes, 3 August 1936, *Archer 3612* (US); Omolas, Matto Grosso, 6 August 1908, *Hoehne 30* (US). **Paraguay**: in regione lacus Ypacaray, May 1913, *Hassler 12654* (F, GH, MO, US); common in a dry lagoa, Tapytá, April 1931, *Jørgensen 4722* (NY, US, F, MO); fluminis Apa, February 1902, *Hassler 8453* (GH, MO).

This is often the largest phase of *E. tenellus*, some of the plants having a scape 35 cm. long, with leaves 20 cm. long and 12 mm. wide (Fig. 76). A collection from Honduras: El Achote, hills above the plains of Siguatepeque, Dept. Comayagua, *Yuncker, Dawson & Youse 6321* (F), has a slight development of a fourth lateral rib on some achenes. This may represent a

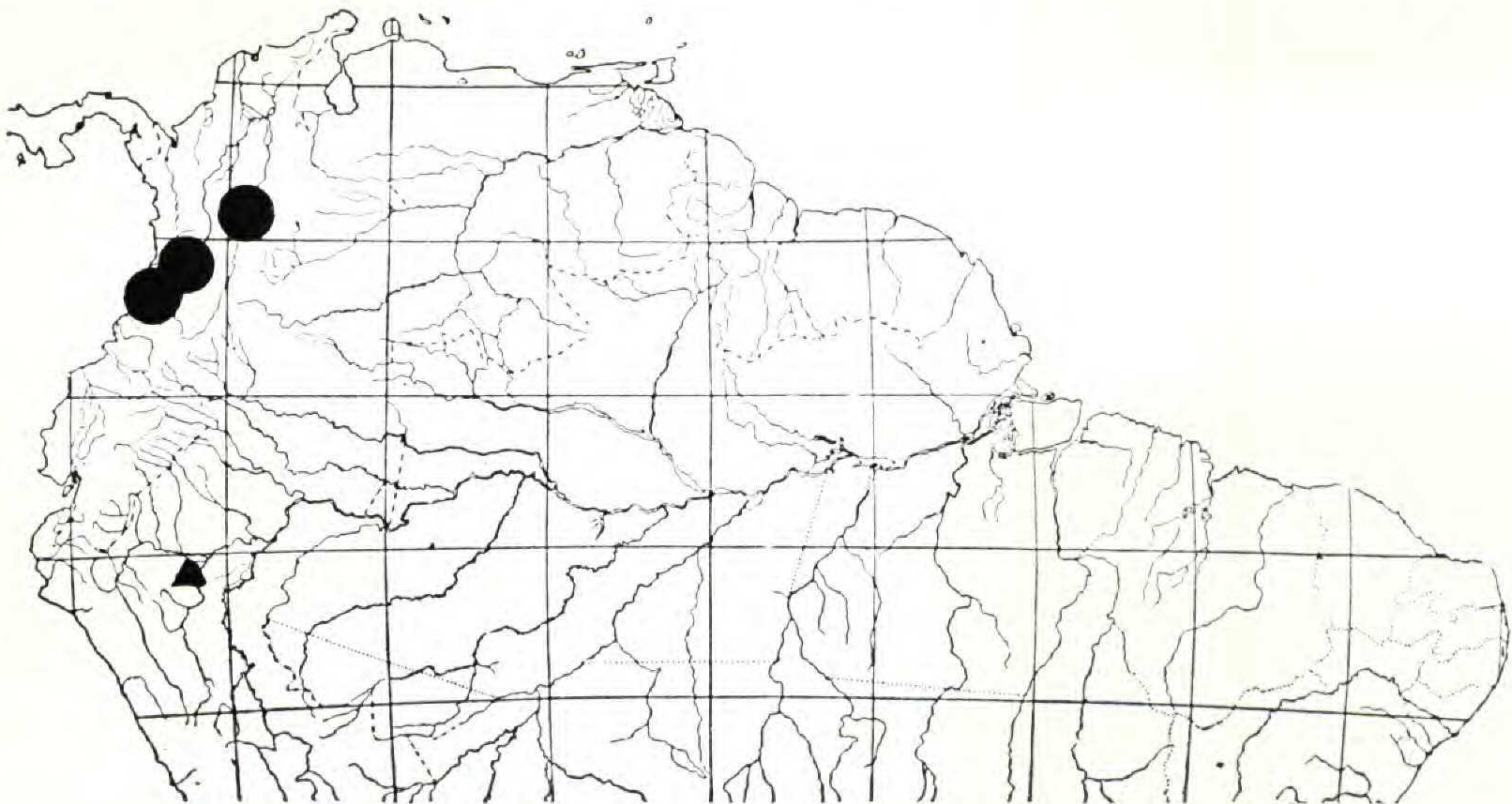


Map 14. *Echinodorus isthmicus*.

slight introgression from populations to the southeastward in Costa Rica, where that character is well-developed.

E. TENELLUS var. *LATIFOLIUS* f. **apanecae** Fassett, n.f., plantae in aqua vadosa; foliis linearibus longis-oblongeolatis, 12–22 cm. longis, flaccidis, membranaceis, ad basim attenuatis.—**El Salvador:** in about 1 foot of very cold water, Lagunita las Ninfas, Apaneca, alt. 5430 ft., 28 January 1951, *Fassett 28704* (GH, wis); shallow water, mud bottom, Laguna Verde, Apaneca, alt. 5100 ft., 28 December 1950, *Fassett 28505* (TYPE in Chicago Natural History Museum, GH); same data, no. 28508 (F); same locality, 30 December 1950, *Fassett 28525* (F).

When the fertile terrestrial form is not found nearby the identification of submersed forms is more difficult. Since *E. tenellus* var. *latifolius* is the only one of this group that has been collected in Central America, these plants presumably belong to



Map 15. *Echinodorus magdalenensis*, dots; *E. quadricostatus*, triangle.

that variety. The leaves are much larger than in the terrestrial forms. A few leaves of no. 28508 are a little more like the terrestrial ones, and show the callous margin and tip characteristic of *E. tenellus*.

16. *ECHINODORAS isthmicus* Fassett, n. sp., foliis lanceolatis, 3–7 cm. longis, 2–5 mm. latis; scapis 6–12 cm. altis, saepe verticillatis; antheris 0.7 mm. longis; achaeniis 1.6 mm. longis, 4-costatis utrinque, rostro nullo aut 0.2 mm. longo (Fig. 69).

Costa Rica and Panama (Map 14). **Costa Rica:** Cienega da Agua Buena, Cañas Gordas, alt. 1100 m., February 1897, *Pittier 11126* (US). **Panama:** wet meadows along Río Caldera, south of El Boquete, alt. 1250 m., 1 March 1918, *Killip 3618* (US—TYPE).

17. *ECHINODORUS quadricostatus* Fassett, n. sp., laminis foliorum 3.5–5 cm. longis, 3–6 mm. latis; achaeniis 1.8 mm. longis, 4-costulatis utrinque (Fig. 72); rostro 0.8 mm. longo; antheris 0.6 mm. longis.

Northern Peru (Map 15, triangle). **Peru:** Dept. Loreto, Balsapuerto, altitude about 220 meters, January 1933, *Klug 2875* (GH—TYPE; US, F); Dept. Loreto, Yurimaguas, lower Río Huallaga, alt. about 135 meters, 22 August—9 September 1929, *Killip & Smith 27963* (US); lower Río Huallaga, Dept. Loreto, October–November 1929, *Williams 4698* (F).

18. *ECHINODORUS magdalenensis* Fassett, n. sp., laminis foliorum lanceolatis, 3–5 cm. longis, 5–9 mm. latis; achaeniis 1.6–1.7 mm. longis, costis obscuris aut obsolete (Fig. 71); rostro 0.6–0.7 mm. longo; antheris 0.4–0.5 mm. longis.

In Colombia, in the basin of Río Magdalena and on the nearby Pacific coast (Map 15, dots). **Colombia:** Department of Antioquia, Puerto Berrio, alt. 130–140 m., 11–13 January 1918, *Pennell 3717* (GH, US), Department of El Valle, Cuchilla, east of Zarzal, alt. 1200–1600 m., 22 July 1922, *Pennell, Killip & Hazen 8523* (US—TYPE); Department of Valle, costa del Pacifico, Isla del Guayabel, en lo desembocadura río Cajambre, 0–5 m. alt., 11 & 12 February 1944, *Cuatrecasas 16229* (US).

IX. DISTRIBUTION OF CHARACTERS IN SECTION TENELLI

The morphological relationships as based on nutlets are shown in Figs. 66–72. Specific distinctions are shown by double lines and varietal by single lines; this is on a basis of how the characters act, not on how different they look. The rounded summit of the achene correlates with the beak poorly developed or absent, and plants with 3-ribbed nutlets are quite distinct from those with 4-ribbed nutlets, but the short beak grades imperceptibly into no beak at all and various intermediates are found between the ribbed achenes and the ribless ones. Nine different combinations of characters are theoretically possible, of which 5 have been found.

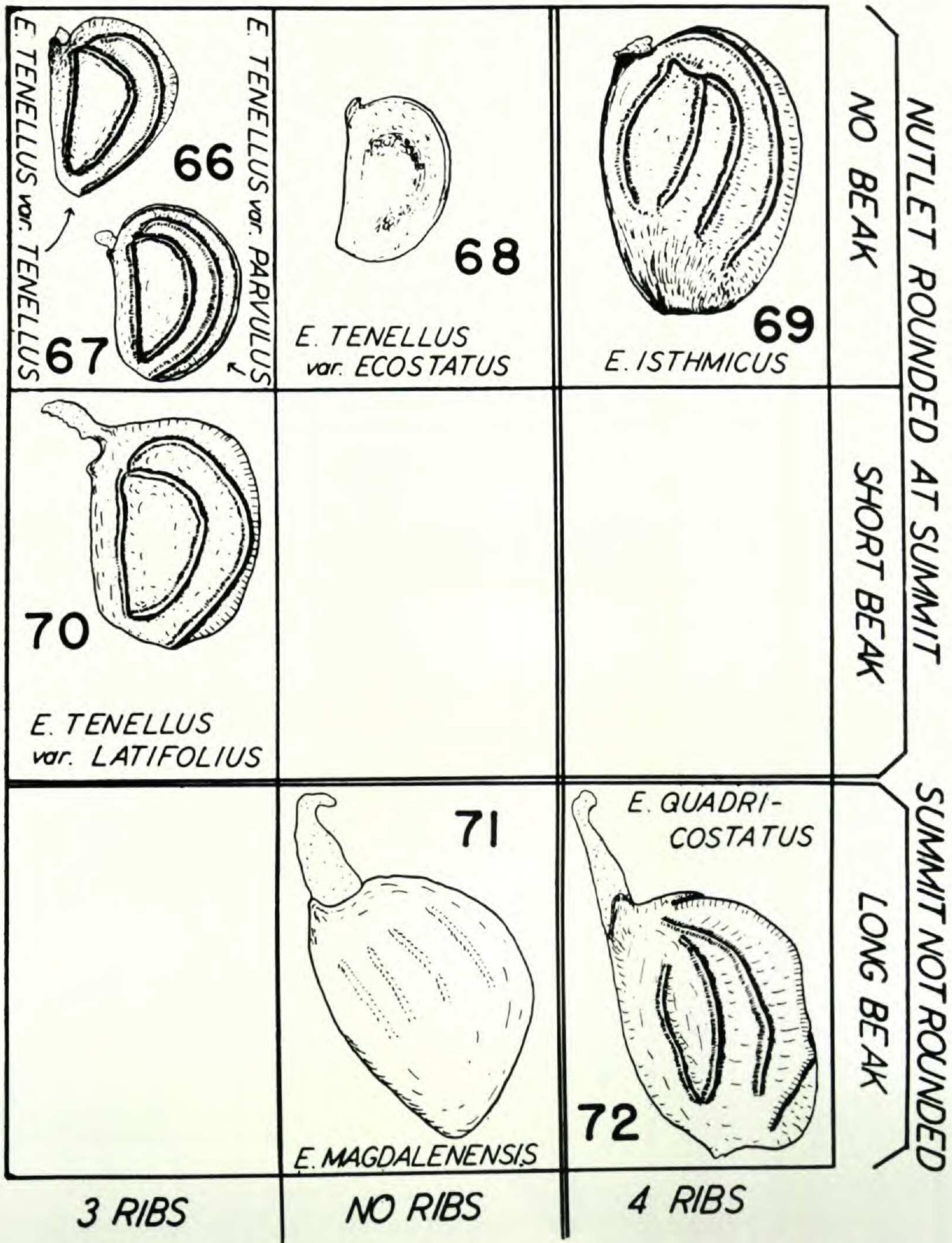
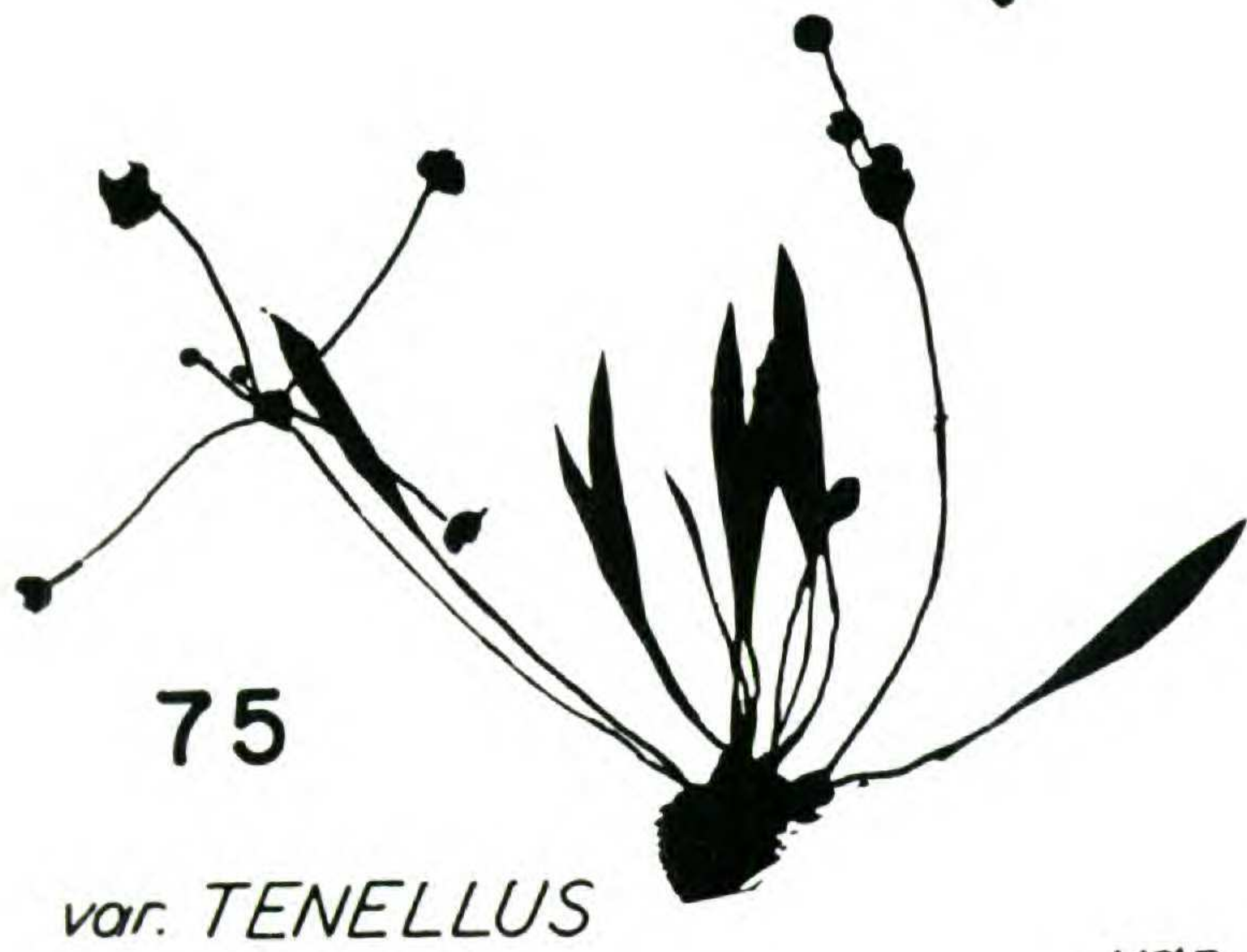
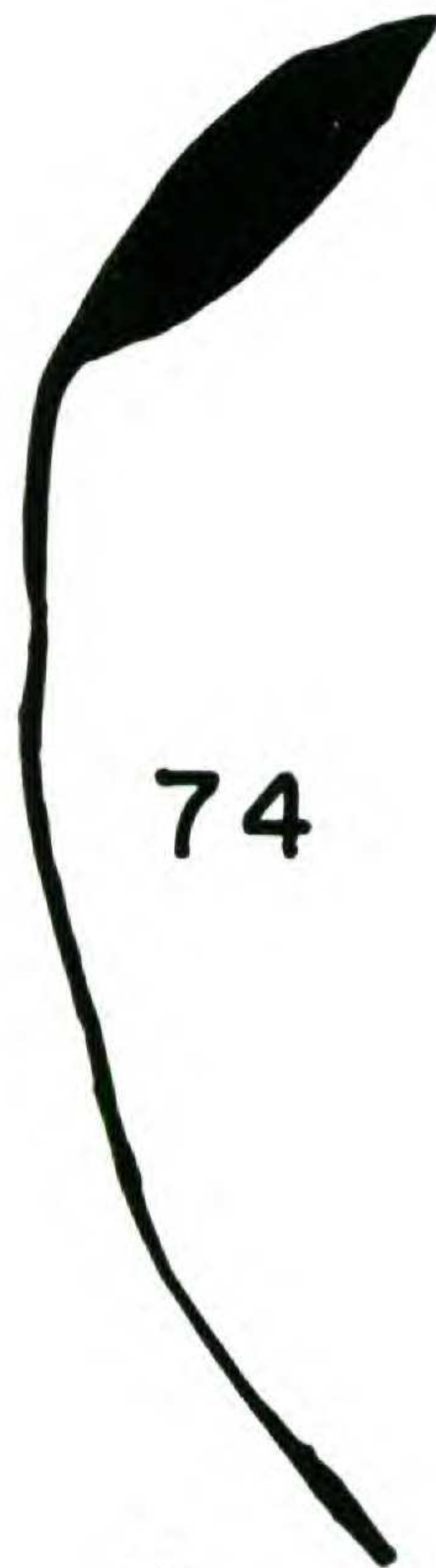
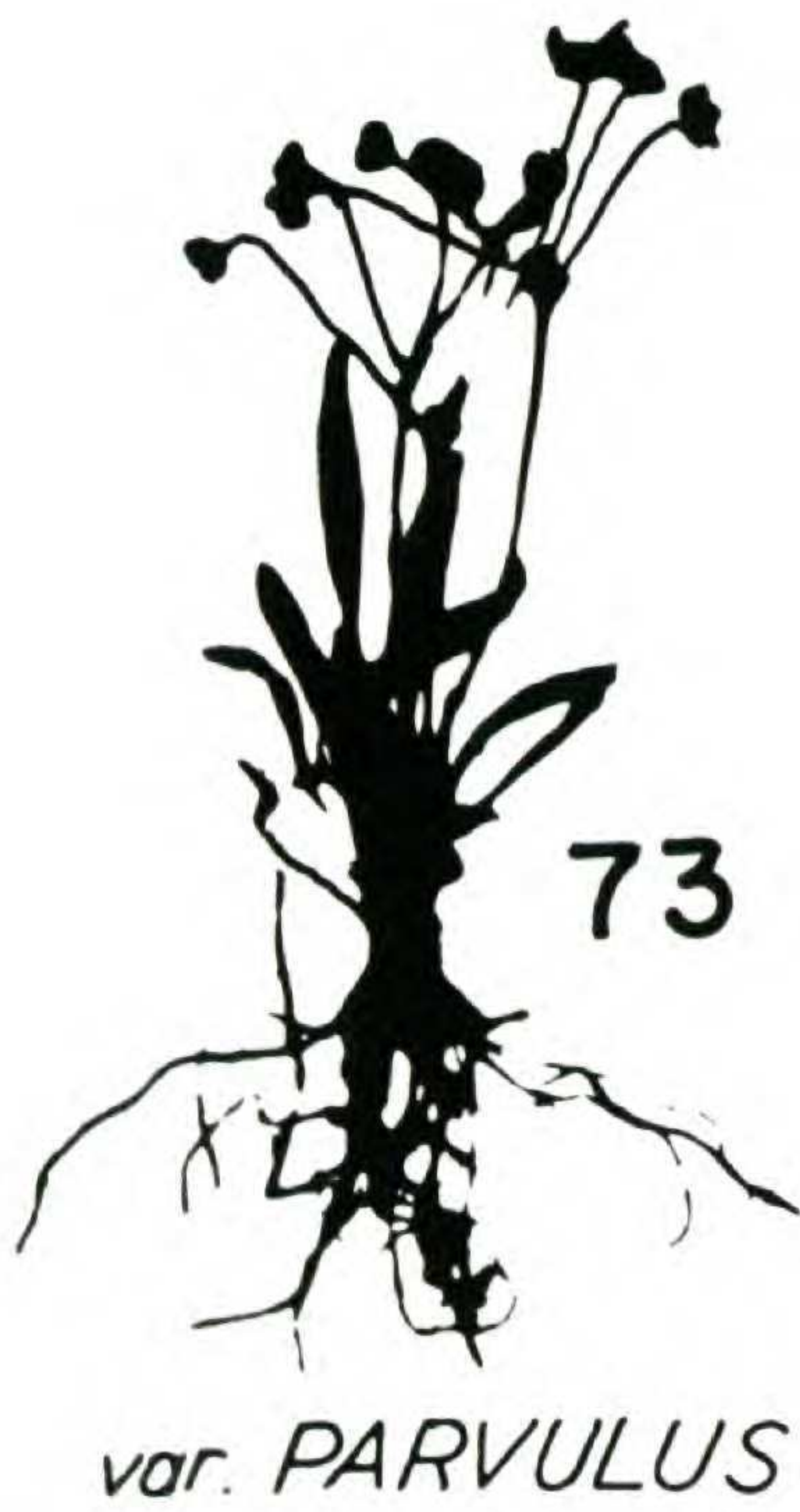


FIG. 66-72. NUTLETS OF SECTION TENELLI (X 20). Fig. 66. *E. tenellus* var. *tenellus*; Brazil, Gardner 2740. Fig. 67. *E. tenellus* var. *parvulus*; Massachusetts, Faxon. Fig. 68. *E. tenellus* var. *ecostatus*; Venezuela, Pittier 11707. Fig. 69. *E. isthmicus*; Panama, Killip 3618. Fig. 70. *E. tenellus* var. *latifolius*; Venezuela, Pittier 5844. Fig. 71. *E. magdalenensis*; Colombia, Pennell 3717. Fig. 72. *E. quadricostatus*. Peru, Killip & Smith 27963. Specimens in United States National Herbarium.



E. TENELLUS

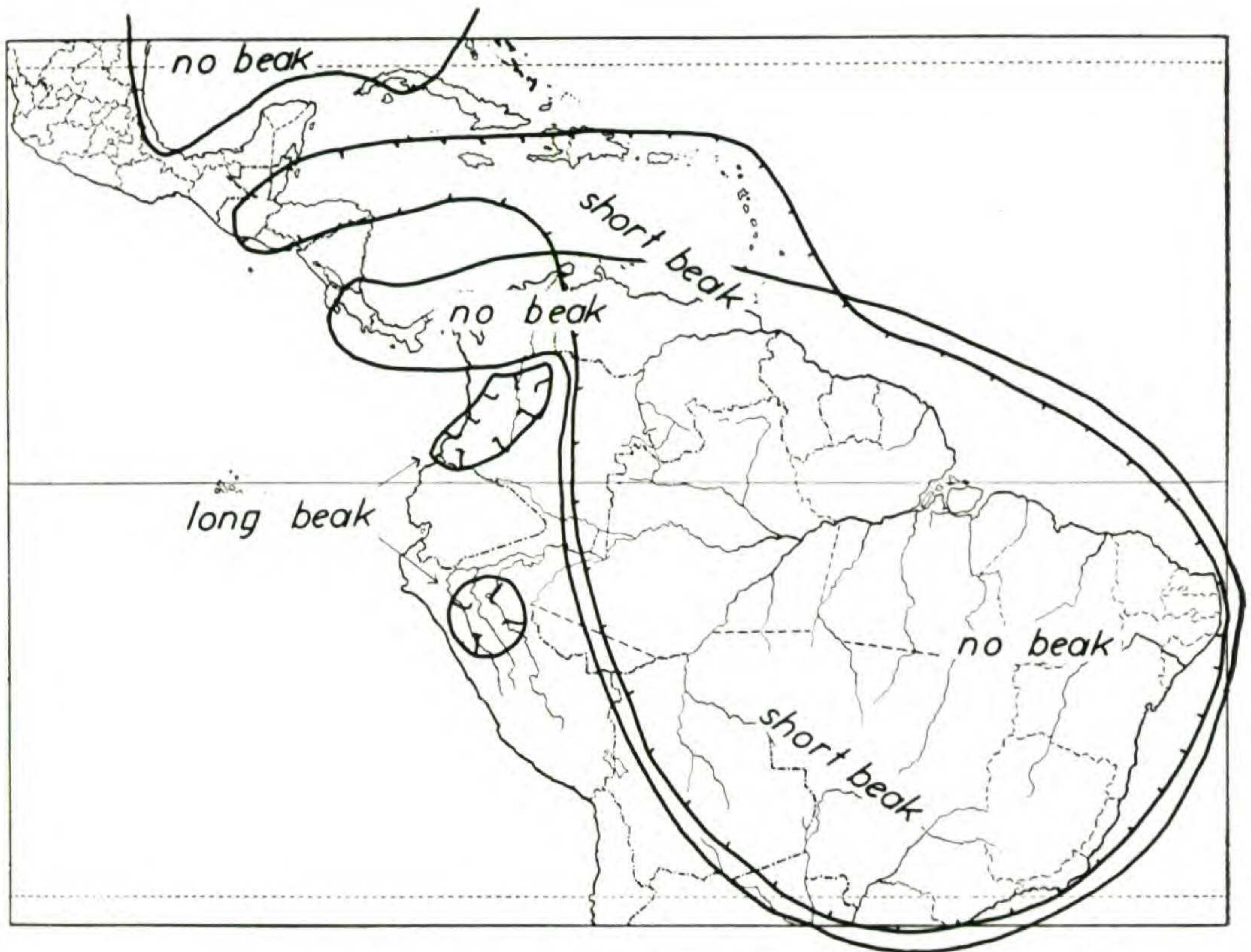
FIG. 73-76. VARIETIES OF *E. TENELLUS*, NATURAL SIZE, LEAVES OR PLANTS, FROM PHOTOGRAPHIC PRINTS OF SPECIMENS IN US. Fig. 73. *Var. parvulus*: Florida, Harper 39. Fig. 74. *Var. parvulus*: Missouri, Eggert. Fig. 75. *Var. tenellus*: Venezuela, Chardon 252. Fig. 76. *Var. latifolius*: Dominican Republic, Ekman 11025.

On Maps 16 & 17, characters are mapped, and on Map 18 the two previous maps are combined to give a map of the recognized taxa.

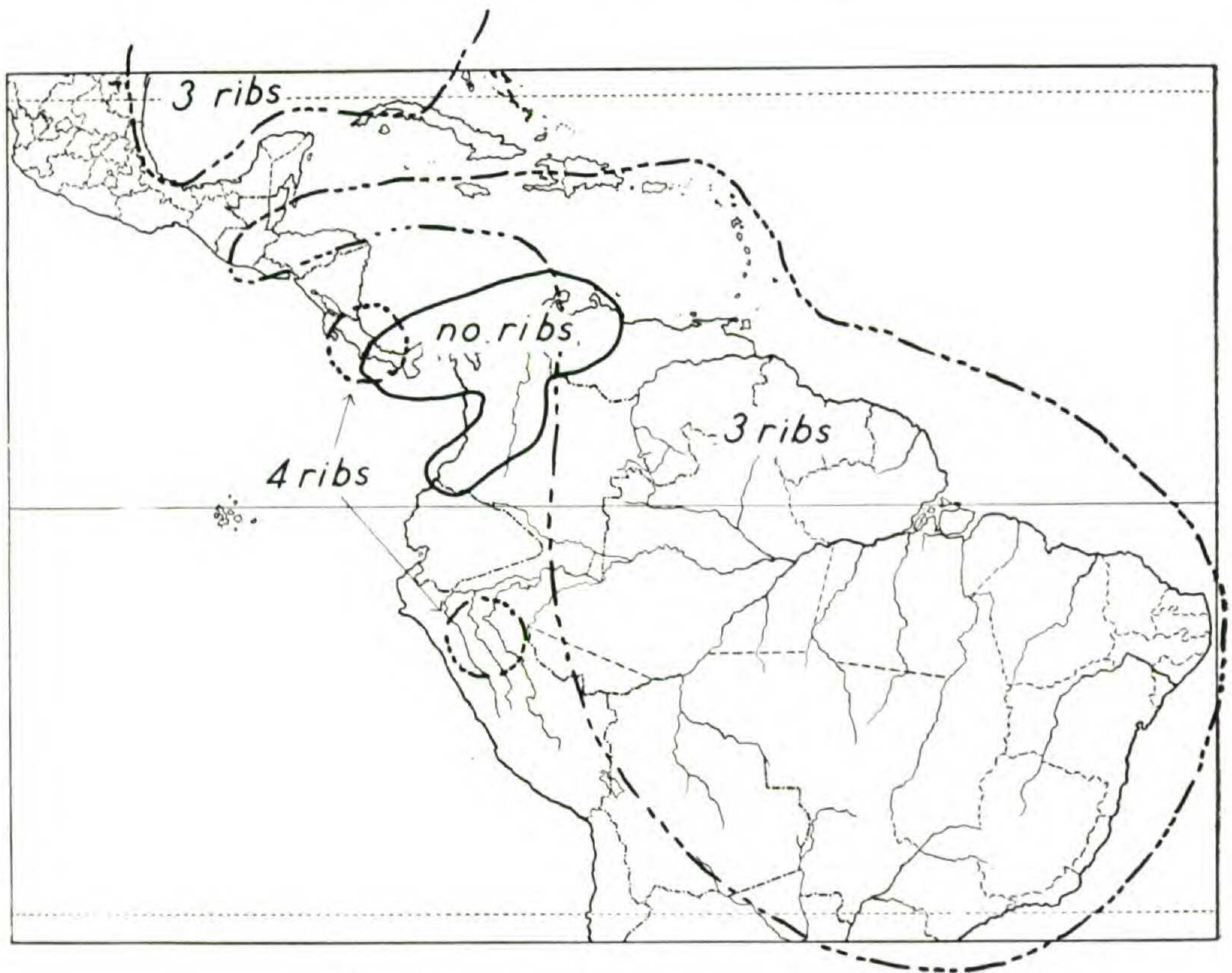
Map 16. The long beak, which is correlated with a sloping summit of the nutlet, is in a relatively small area in the northern Andean region. The short beak and undeveloped beak both occur in a great area centering on the Amazon basin, but from this region of coexistence they reach out in slightly different directions; the short beak follows the geologically ancient route through the Antilles to northern Central America, while the undeveloped beak runs from northern South America into the younger lands of the Isthmus of Panama. The undeveloped beak then reappears in western Cuba and Mexico, ranging thence northward on the Atlantic Coastal Plain to Massachusetts and in the Mississippi embayment to Missouri.

Map 17. The species with 4 ribs on the nutlet have been found in Peru (altitude 135–220 meters) and in Costa Rica and Panama (1199–1250 meters). More widespread is the nutlet with 3 ribs. Lack of ribs is confined to the lowlands from Venezuela and Colombia to Panama; the ribless condition blends on the one hand with the 3-ribbed phase to produce *E. tenellus* var. *ecostatus* (Fig. 68) and combines on the other hand with the 4-ribbed long-beaked *E. quadricostatus* type to produce *E. magdalenensis* (Fig. 71).

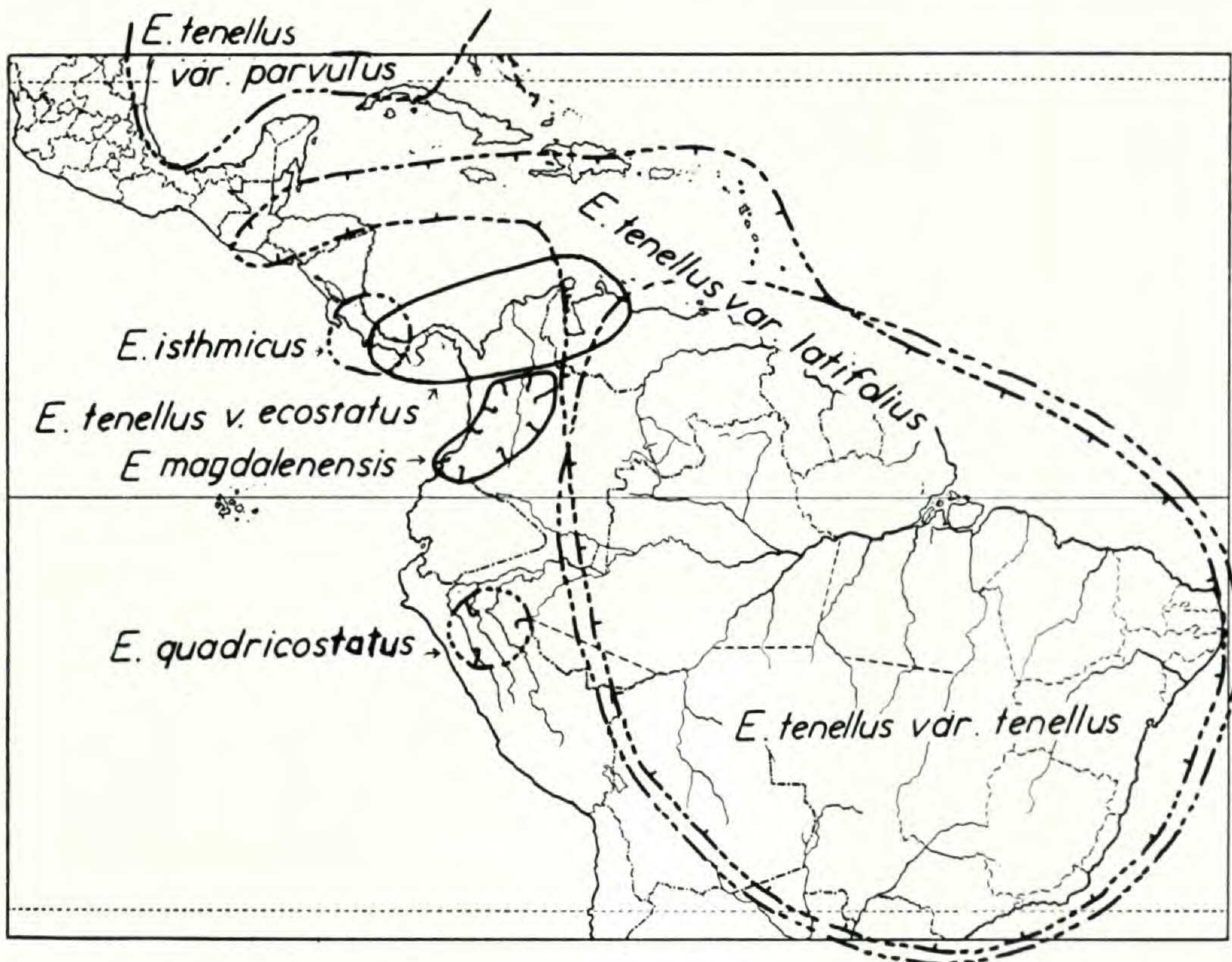
From the morphological relationships shown in Figs. 66–72, and the geographical relationships shown in Maps 16–18, we may speculate concerning phylogenetic relationships. Phylogeny is, as is so often the case, more susceptible to speculation than to proof. If we hypothesize as ancestral types *E. tenellus* var. *tenellus* (Fig. 66) mainly of the Amazon basin, and *E. quadricostatus* (Fig. 72) of the headwaters of the Amazon, we may then see *E. tenellus* var. *latifolius* (Fig. 70) as deriving its beak from *E. quadricostatus*. Var. *latifolius* then spreads through the range of var. *tenellus* and beyond it through the Antilles to Central America. As for *E. tenellus* var. *ecostatus* and *E. magdalenensis*, these occupy contiguous areas and are both characterized by partial or complete suppression of ribs; when there is some suggestion of ribs, *E. tenellus* var. *ecostatus* shows 3 and *E. magdalenensis* shows 4. It seems unlikely that



Map 16. Distribution of beak types.



Map 17. Distribution of rib types.



Map 18. Composite of maps 16 and 17 to show distribution of taxa.

the same habit of rib suppression should have originated independently in two species in adjacent areas. The greater constancy of rib suppression in *E. magdalenensis* suggests that that species arose first, perhaps by mutation from an *E. quadricostatus* stock, and that its character has subsequently been transmitted to an *E. tenellus* stock in the geologically young lowlands of Venezuela and adjacent Panama. *E. isthmicus* may be composed of another recombination of the characters of *E. tenellus* and *E. magdalenensis*.

Another hypothesis is suggested by my colleague Dr. Jonathan Sauer, involving *E. magdalenensis* (Fig. 71) as a primitive type, with a genetic make-up involving 4 ribs but with the factor for ribs suppressed; this would involve the origin of *E. quadricostatus* (Fig. 72) from *E. magdalenensis* and an *E. tenellus* stock to introduce expression of the factor for ribs, and of *E. isthmicus* (Fig. 69) and *E. tenellus* var. *ecostatus* (Fig. 68) from different combinations of characters of *E. magdalenensis* and *E. tenellus*.

V. KEYS FOR IDENTIFICATION IN LIMITED AREAS

ECHINODORUS IN THE UNITED STATES

- a. Slender plants rarely 10 cm. high; carpels 20 or fewer in a loose head; stamens 6 or 9; anthers basifixed; nutlets beakless (Fig. 67).
E. tenellus var. *parvulus*.
- a. Robust plants with ovate or cordate leaves (except for dwarfed individuals on drying shores); carpels many in dense heads; stamens 9–30; anthers versatile; nutlets beaked (23–29).
- b. Sepals with smooth veins; profile of fruiting head appearing echinate to the naked eye, due to the long (0.5–1.8 mm.) beaks on the nutlets; each side of nutlet with 5 arching ribs of which the 2 wing-like ones are alternate with the others; glands of nutlet acuminate at the upper end and entering the base of the beak (Figs. 25–29); pellucid lines of leaves mostly less than 1 mm. apart and often several mm. long (Fig. 55); scape erect with whorled and usually compound branches.
- c. Beak of nutlet 1.2–2.0 mm. long, $\frac{1}{2}$ – $\frac{2}{3}$ as long as the body (Figs. 25–27); anthers 0.8–1.2 mm. long. *E. Berteroi* var. *Berteroi*.
- c. Beak of nutlet 0.5–0.8(–1.0) mm. long, $\frac{1}{3}$ – $\frac{1}{2}$ as long as the body (Figs. 28, 29); anthers 0.5–0.8 mm. long. . . . *E. Berteroi* var. *lanceolatus*.
- b. Sepals with papillose ridges; profile of fruiting heads appearing nearly smooth due to the short (0.2–0.8 mm.) beaks on the nutlets; each side of nutlet with 3–4 abruptly curved and sometimes joining ribs of which the 1 or 2 toward the dorsal edge are wing-like toward the tip (Figs. 23, 24); glands of nutlet rounded at both ends and not closely approaching the beak; pellucid lines of leaves mostly 1 mm. or more apart and rarely exceeding 1 mm. in length (Fig. 54); scape erect when young but soon procumbent, with verticillate peduncles at the nodes. *E. cordifolius*.

ECHINODORUS IN THE WEST INDIES

- a. Carpels 20 or fewer in a loose head; stamens 6–9; anthers basifixed.
- b. Leaves narrowly lanceolate or elliptic (Fig. 76); ribs of nutlets not crested (Fig. 70). *E. tenellus* var. *latifolius*.
- b. Leaves cordate; ribs of nutlets crested (Fig. 53). . . . *E. nymphaeifolius*.
- a. Carpels many in a dense head; stamens 9–30; anthers versatile.
- c. Veins of leaf radiating from base of the blade (Figs. 2, 3, 10); petiole terete or fluted, not 2-winged.
- d. Beak more than $\frac{1}{2}$ as long as the body of the nutlet (Figs. 25–27), with tapering apex of glands entering its base; pellucid lines of leaves crowded, often several mm. long (Fig. 55). . . . *E. Berteroi* var. *Berteroi*.
- d. Beak shorter, the rounded ends of the glands not reaching its base (Figs. 30, 31, 40); leaves with more scattered pellucid short lines (Figs. 57–58) or dots (Fig. 56).
- e. Blades with stellate hairs toward the base, about as wide as long (Fig. 10).
- f. Blades with pellucid dots and few or no very short lines (Fig. 56), petals white. *E. grandiflorus* var. *grandiflorus*.
- f. Blades with pellucid lines 0.2–0.5 mm. long; flowers yellow.
E. grandiflorus var. *aureus*.
- e. Blades glabrous, about twice as long as wide (Fig. 13). . . . *E. ovalis*.
- c. Upper pair of veins paralleling the midrib for some distance (Fig. 16); petiole winged. *E. Grisebachii*.

ECHINODORUS IN MEXICO

- a. Carpels 10 or fewer in a loose head; stamens 6–9; anthers basifixed.
- b. Leaves narrowly lanceolate or elliptic (Fig. 73, 74); ribs of nutlet not crested (Fig. 67) *E. tenellus* var. *parvulus*.
- b. Leaves cordate; ribs of nutlet crested (Fig. 53) *E. nymphaeifolius*.
- a. Carpels many in a dense head; stamens 9–30; anthers versatile.
- c. Petiole terete or fluted, not winged (Figs. 1–5), blades with clear pellucid dots or lines.
- d. Leaves glabrous, with pellucid lines (Fig. 55).
- e. Nutlets about $\frac{2}{3}$ as wide as long, the summit rounded on one side (Fig. 22), with very short beak and round facial glands . . . *E. virgatus*.
- e. Nutlet twice as long as wide, tapered to the very long beak (Figs. 25–27), the facial glands tapered at apex to enter the base of the beak *E. Berteroi* var. *Berteroi*.
- d. Leaves with stellate hairs and pellucid dots (Fig. 56).
E. grandiflorus var. *grandiflorus*.
- c. Petiole winged (Figs. 14, 15); blades with very obscure pellucid lines or none *E. Andrieuxi*.

ECHINODORUS IN CENTRAL AMERICA

- a. Carpels 20 or fewer in a loose head; stamens 6–9; anthers basifixed.
- b. Leaves narrowly lanceolate or elliptic (Figs. 75, 76); ribs of nutlet not crested (Figs. 68–70).
- c. Facial ribs 3 on each side (Fig. 70), or absent (Fig. 68).
- d. Facial ribs nearly or quite suppressed (Fig. 68); nutlets 0.9–1.1 mm. long; styler beak absent or nearly so *E. tenellus* var. *ecostatus*.
- d. Facial ribs well developed (Fig. 70); nutlets 1.4–1.8 mm. long; styler beak 0.2–0.5 mm. long *E. tenellus* var. *latifolius*.
- c. Facial ribs 4 on each side (Fig. 69) *E. isthmicus*.
- b. Leaves cordate; ribs of nutlets crested (Fig. 53) *E. nymphaeifolius*.
- a. Carpels many in a dense head; stamens 9–30; anthers versatile.
- e. Sepals 12–20-nerved, thin, withering, not accrescent, reflexed or loosely ascending in fruit, pellucid markings of leaves, if present, not reticulate.
- f. Leaves with blades cordate at base (Figs. 10–12); petioles terete or fluted, not winged; base of blades and summit of petioles with stellate hairs or muricate (Fig. 11).
- g. Flowers pedicelled; blades with few or no pellucid lines, sometimes with pellucid dots.
- h. Blades with copious pellucid dots (Fig. 56)
E. grandiflorus var. *grandiflorus*.
- h. Blades without pellucid markings *E. muricatus*.
- g. Flowers sessile; blades with very short pellucid lines (Fig. 60).
E. bracteatus var. *bracteatus*.
- f. Leaves glabrous, with blades tapered (Figs. 14, 16) or subcordate (Fig. 15) at base; petioles 2-winged.
- i. Veins radiating from the base of the blade (Figs. 14, 15); leaves with pellucid lines very obscure or absent; nutlets long-beaked, with 1 facial gland (Figs. 41–43) *E. Andrieuxi*.
- i. Upper pair of veins paralleling the midrib for some distance (Fig. 16); leaves with well-marked pellucid lines (Fig. 63); nutlets short-beaked, with several facial glands (Fig. 51) *E. Grisebachii*.
- e. Sepals about 30-nerved, thick and brittle, enlarging in fruit to cover the fruiting head; pellucid markings reticulate (Fig. 64) *E. tunicatus*.

ECHINODORUS IN TROPICAL SOUTH AMERICA

- a. Slender plants rarely 10 cm. high; carpels 20 or fewer in a loose head; stamens 6 or 9; anthers basifixed.
- b. Summit of nutlet rounded above the beaklet (Figs. 66, 68, 70); stylar beak 0.5 mm. or less long; facial ribs of nutlet present or absent.
- c. Nutlet 0.9–1.1 mm. long; stylar beak nearly absent; anther 0.2–0.6 mm. long.
- d. Facial ribs well developed (Fig. 66).....*E. tenellus* var. *tenellus*.
- d. Facial ribs nearly or quite suppressed (Fig. 68).
E. tenellus var. *ecostatus*.
- c. Nutlet 1.4–1.8 mm. long; stylar beak 0.2–0.5 mm. long (Fig. 70); anther 0.5–1.0 mm. long.....*E. tenellus* var. *latifolius*.
- b. Summit of nutlet horizontal or sloping downward from the beaklet (Fig. 71); stylar beak 0.6–0.7 mm. long; facial ribs of nutlet nearly or quite obsolete.....*E. magdalenensis*.
- a. Robust plants usually 50 cm. or more high; carpels many in dense heads; stamens 9–30; anthers versatile.
- e. Leaves with blades more or less cordate at base (Figs. 10–12); petiole terete or fluted but not 2-winged; leaves mostly stellate-pubescent or muricate about summit of petiole and base of blade.
- f. Flowers long-pedicelled.
- g. Blades with pellucid dots (Fig. 56).....*E. grandiflorus* var. *grandiflorus*.
- g. Blades without pellucid markings.
- h. Inflorescence erect, often compound, with pedicels reaching 3 cm. in length.....*E. muricatus*.
- h. Scape creeping, simple, sometimes 2 m. long, rooting at nodes and sometimes proliferous, with erect pedicels sometimes reaching 7 cm.....*E. fluitans*.
- f. Flowers nearly sessile.
- i. Leaves with very short pellucid lines (Fig. 60) and stellate hairs.
E. bracteatus var. *bracteatus*.
- i. Leaves glabrous and without pellucid markings.
E. bracteatus var. *efenestratus*.
- e. Blades tapered (Figs. 18–21) or truncate (Fig. 17) at base; petioles 2-winged.
- j. Veins radiating from the base of the blade (Figs. 17–20); internodes of inflorescence sharply keeled but not winged.....*E. paniculatus*.
- j. Upper pair of veins running parallel to the midrib for some distance (Fig. 21); internodes of inflorescence with 3 herbaceous wings about 2 mm. wide.....*E. trialatus*.

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